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# Plant productivity: a predictor of animal species and community characteristics

Ecological patterns from local to global scale

**Birgitta Aava-Olsson**



# Plant productivity: a predictor of animal species and community characteristics

*Patterns from local to global scale*

Birgitta Aava-Olsson

Akademisk avhandling som för vinnande av filosofie doktorsexamen kommer att offentliggöras i hörsal Björken SLU, Umeå, fredagen den 21 september, 2001, kl. 10.00.

## Abstract

This thesis focus on the effects of plant productivity on various aspects of geographic range size, resource use, body size and abundance of animal species from different taxa, from a local to a global scale. The aim was to identify putative scales to determine whether it is possible to find functional links between plant productivity and species richness by considering how productivity affects species characteristics for different assemblages, *e.g.* mammals, insects and birds.

Terrestrial endemic mammal genera in the world appeared to be most common in zoogeographic regions of intermediate plant productivity (Paper I). I could not find evidence that Australian herbivorous mammals either combine food resources in more ways or are more selective in areas of high plant productivity (Paper II). Although, these Australian herbivorous mammals were larger and more similar in size in biomes of high plant productivity than in low (Paper III). I further, found that for two families of ground dwelling Coleoptera plant productivity does not have any effect on the relationship between number of individuals and number of species within body size classes in local forest sites (Paper IV). There was a trend that higher productivity sites could hold more individuals of large sized species, but not more species. The reverse trend was observed for small sized species. Breeding forest birds in Sweden had highest average densities in areas of both low and high plant productivity (Paper V). Also, species with a lower abundance than expected from their range size were mainly found in areas of high plant productivity while the reverse was true for species with higher than expected abundance.

Finding functional links between observed patterns of animal characteristics and between species richness and productivity are vital to our understanding of how the transfer of energy from plants to animals affects the distribution of species. The spatial scale at which to study the mechanisms does influence how these proposed functional links will be affected by productivity. In this thesis I show that changes in productivity are likely to induce complex interactive changes in all key attributes, rather than clear linear responses. I therefore suggest that future studies should consider all these attributes in conjunction.

*Key words:* plant productivity, range size, resource use, body size, abundance, endemism, species richness, mammals, insects, birds, forests, scale.

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Ecological patterns from local to global scale

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Key words: plant productivity, range size, resource use, body size, abundance, endemism, species richness, mammals, insects, birds, forests, scale.

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# Appendix

## Papers I-V

The thesis is based on the following papers, which will be referred to by the corresponding Roman numerals in the text.

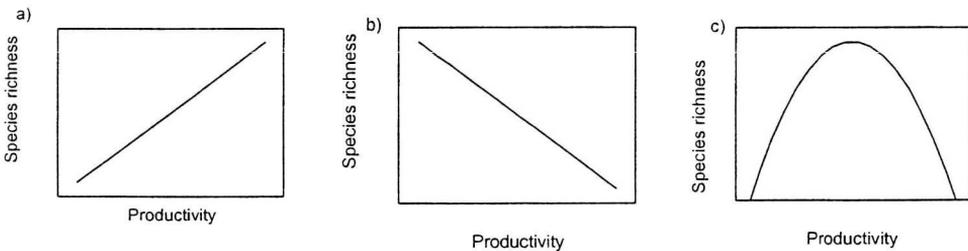
- I. Danell, K. and Aava-Olsson, B. (2001). Endemic mammalian genera: Are they really unique? *Journal of Biogeography*. submitted manuscript
- II. Aava, B. (2001). Can resource use be the link between productivity and species richness in mammals? *Biodiversity and Conservation* in press
- III. Aava, B. (2001). Primary productivity can affect mammalian body size frequency distributions. *Oikos* 93: 205-212
- IV. Aava-Olsson, B. Rove beetles (Staphylinidae), ground beetles (Carabidae) and energy availability: How are density and species richness of body sizes related to plant productivity? Manuscript
- V. Aava-Olsson, B., Albrechtsen, B. and Svensson, S. Abundance – range size relationships are obscured by environmental and species specific variation. Manuscript

Papers I, II and III are reproduced with kind permission from the publisher

# Introduction

The distribution of animal species in the world today is neither regular nor random. Some areas are more diverse than others and the composition of species differs from place to place. Immigration, emigration, speciation and extinction are all important processes that help shape the composition at any one location. They are all significant, although their relative importance varies at different scales (Huston 1999), and are affected by environmental conditions.

Plant productivity has been suggested as an essential environmental factor. Several studies have shown that plant productivity affects the diversity of species within both plant and animal taxa (Abramsky & Rosenzweig 1984, Turner et al. 1987, Owen 1988, Adams & Woodward 1989, Currie 1991, Eggleton et al. 1994, Kaspari et al. 2000, Lennon et al. 2000). Depending on spatial scale, habitat type, taxonomic and trophic affiliation, species richness either increases, decreases or shows a unimodal relationship (fig.1) with increasing plant productivity (Waide et al. 1999). Decreasing relations are rare in animal taxa but quite common for plants (Huston 1994) and has been attributed to the increasing dominance by a few species over the others due to increasing nutrient concentrations, termed 'the paradox of enrichment' by Rosenzweig (Rosenzweig 1971).



*Fig. 1* Schematic diagrams showing three general types of relations between productivity and species richness.

If, in fact, species richness is functionally dependent on plant productivity it is important to understand how species are affected morphologically, physiologically and ecologically by plant productivity. This can be done by examining the effect of plant productivity on species' characters such as the sizes of their range, population and bodies, and their use of resources. These are all important features of species, and if there is a functional explanation underlying

productivity-richness relationships then productivity must also affect them in some way.

A number of hypotheses have been put forward to explain the relationship between plant productivity and species richness. Postulated mechanisms include interspecific competition, evolutionary immaturity, predator-prey ratios, changes in environmental heterogeneity, disturbance and area (Rosenzweig & Abramsky 1993, Abrams 1995, Srivastava & Lawton 1998). There are at least three mechanistic hypotheses that aspire to explain this relationship. I will briefly summarise them here as a background for the discussions of the relationships between plant productivity and range size, resource use, body size and abundance.

The first one is the 'energy limitation' hypothesis, which states that energy limits the number of individuals that can be sustained in a habitat (Wright 1983, Currie 1991). If plant productivity increases in a given area, the amount of energy available for consumer species increases and thus more individuals will be able to inhabit that area. When the number of individuals increases, so will the number of species as a consequence. The result is a constant increase in species richness with increasing plant productivity (Fig. 1a).

The second hypothesis is the 'environmental heterogeneity' hypothesis (Abrams 1988). This hypothesis holds that when productivity is low the landscape will be uniformly barren and the existing resources homogenous. Under these conditions very few species can exist. As plant productivity rises, plant diversity will increase, making resources more heterogeneous for animals. This allows for a greater species richness of animals. Beyond a certain point along the productivity gradient plant diversity may decline as a result of increasing dominance by a few plant species. When this happens resources become less heterogeneous again and animal diversity drops. The result is a hump-shaped relationship between plant productivity and species richness of animals (Fig. 1c). Alternatively, there may be no increase in dominance, but instead diversity among plants may constantly rise as productivity increases. In this case animal species richness increases constantly with productivity (Fig. 1a).

The last hypothesis is the 'more specialisation' hypothesis, which argues that productivity increases the abundance of rare resources or conditions that specialist species are dependent upon, enabling these species to exist (Schoener 1976, Abrams 1988, DeAngelis 1995). Thus total species richness increases with productivity (Fig. 1a).

These hypotheses were not directly tested here, but they provided a basis for the rationale underlying the questions I aimed to address.

# Objectives

The studies described in this thesis were designed to examine how the body size, range size, abundance of resources, and their use by species are related to plant productivity at different geographic scales. The principal objective was to identify putative scales, from local to global. By this I aim to determine whether it is possible to find functional links between plant productivity and species richness for different animal assemblages, i.e. mammals, insects and birds.

To put the thesis in the right perspective I first define the variables that I have selected as important characteristics of species (range size, resource use, body size and abundance) affected by plant productivity. Plant productivity is defined in the Encyclopedia of Ecology & Environmental Management (Callow 1998) as "The rate of biomass formed by a plant community per unit surface area of ground, reported as grams dry matter m<sup>2</sup>year<sup>-1</sup>". Many different estimates of energy availability, such as for instance precipitation, evapotranspiration, radiation, net primary productivity, have been used for determining the effects of plant productivity on diversity (Abramsky and Rosenzweig 1984, Turner et al. 1987, Owen 1988, Currie 1991, Eggleton et al. 1994, Kerr & Packer 1997, Andrews & O'Brien 2000). It is, however, important that for instance plant productivity is used to predict the diversity of the plants themselves (Srivastava and Lawton 1998). In this thesis I aim to disentangle how characteristics of animals are affected by energy availability and therefore I have consequently chosen to use plant productivity as the predictor variable.

## Theoretical framework

### Range size

Species differ in the size of the areas their distribution covers. A few species within some taxa are distributed over vast areas, even globally, but most species have a much more restricted ranges. The range size of a species is affected by many different factors, such as the availability of suitable habitat, dispersal ability, competition, predation, historical and evolutionary processes and various climatic and environmental parameters (Gaston 1996).

Of all known species the most sensitive to environmental factors may be ones that have very restricted geographic ranges, i.e. the endemic species. They are highly dependent on how the distribution of key environmental factors are distributed in space and time. Studies have shown that endemic species of various aquatic taxa are restricted to low productive areas (Gronns et al. 1992, Oberdorff et al. 1999, Reaka-Kudla 2000). Furthermore, areas of high endemism

among plants are also characterised by extremely low productivity (Huston 1994). Huston suggested that endemic species are able to survive in low productive environments due to low rates of competitive displacement in these non-equilibrium environments that are characterised by frequent disturbances. The pattern for terrestrial animals however, is not clear as yet. If terrestrial endemic animals are characterised by low competitive ability, they may be found in low productive areas as well. In that case low productive areas may be considered as centres of endemism (Thirgood & Heath 1994).

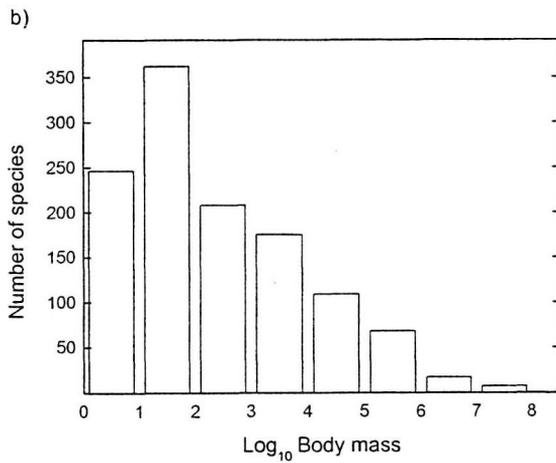
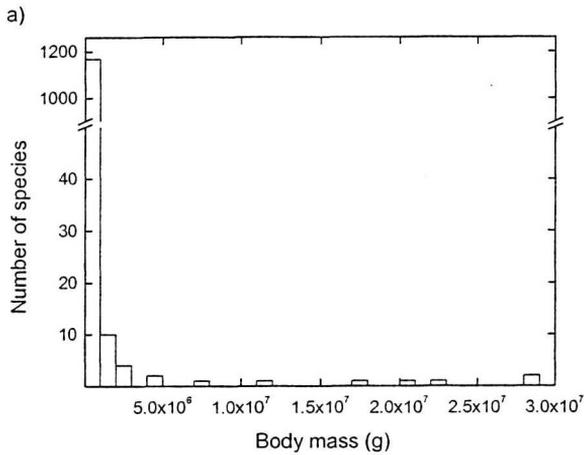
## **Resource use**

Resource use is not only important as a determinant of range size but it also affects the kind of assemblage one might find in high or low productivity areas, respectively. Some species use only a few types of food resources while others include a greater variety in their diet. If resource availability increases with increasing plant productivity, the possibilities for animal species with slightly different food preferences to co-exist also increase. Therefore, the number of ways to combine resources should be higher in high productive regions than in low productive regions. Thereby, also the possibility of an increased species richness.

Increasing energy availability can also increase the density of specialist species (see hypothesis number three in the Introduction), which will be able to persist as viable populations. Based on these arguments we should expect more specialisation among animal species in areas of high plant productivity. This may, according to the 'more specialisation' hypothesis, lead to higher species richness.

## **Body size**

Resource use is also connected with the body size of the animal species. When the average size of all species within a taxon at a large geographic scale, e.g. biome/continental or global, is compared we find that most species tend to be small-bodied (Fig 2a). If the distribution of body sizes is logarithmically transformed it will still be skewed towards larger body sizes (fig 2b). It is not the absolutely smallest species within a taxon that are most numerous, but species with average sizes just greater than the smallest.



*Fig. 2* Body mass of all mammalian genera in the world, (a) actual body mass and (b) log<sub>10</sub> transformed body mass. Even after transformation the distribution is skewed (data from paper I).

The reason to shy not the smallest species are the most numerous can be that there is a trade-off in life-history characters linked to body size that somehow limits the frequency of species in each size class (Charnov 1993, Kozlowski 1996). Reproductive rates have proven to be negatively related to body size, i.e. larger bodied species tend to produce fewer offspring per unit time than those with smaller bodies (Peters 1983, Calder III 1984). Individual growth rate is also related to body size, albeit positively (Peters 1983, Calder III 1984). A trade-off (Figure 3) between these two characters gives an optimal size that is located at the same size as the most numerous size class (Brown et al. 1993). However, this requires energy to be unlimited in the habitat, which is highly unlikely in reality. In low productive areas resources are so scarce that in order to co-exist species must be of different size (Brown 1995). Therefore, I hypothesis that there will be wider size distributions in low- than in high- productivity biomes or continents. As energy availability increases, all individuals can acquire more energy for growth and thus the mean body size of species will be higher in high energy areas than in low energy areas.

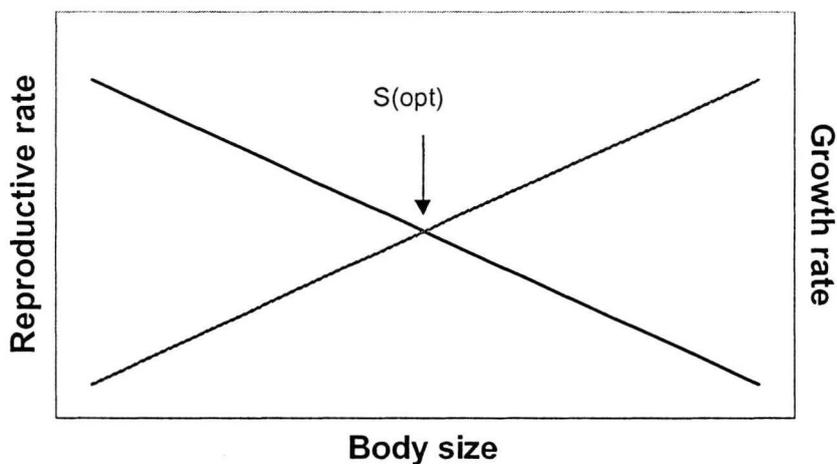


Fig. 3. The optimal body size,  $S(\text{opt})$ , is a trade-off between reproductive rate (decreasing with body size) and growth rate (increasing with body size).

Body size has been suggested to affect the population size of species (Damuth 1981, Peters 1983, Peters & Wassenberg 1983, Brown & Maurer 1987, Morse et al. 1988). Larger species have on average lower population densities than smaller species. However, within local assemblages, as body size decreases the variation in abundance increases because there are more small sized species (Blackburn et al. 1993). The shape of the relationship between body size and abundance has been claimed to be a consequence of energy control (Damuth

1981, Nee et al. 1991, Marquet et al. 1995, Maurer & Brown 1998). By this, population energy use is determined by individual energy use multiplied by the number of individuals of that species. The size class that by this definition uses most of the available energy will be most abundant. However, there is also a variation of sizes among individuals within each species and, consequently, not all individuals of a species will use the same amount of energy. Therefore it is better to group species into different size classes instead of assuming an average body size of species (Cousins 1991).

For local assemblages species richness of different size classes within a taxon has been shown to be related to abundance by a power function:

$$S = I^{0.5}$$

Where S is the number of species in each size class and I is the number of individuals in the same size class (Siemann et al. 1996, Siemann et al. 1999) (Hall & Greenstreet 1996, Gregory 1998). Since the power of this relationship is lower than one, the number of species in increasingly individual rich size classes will eventually reach an asymptote.

Plant productivity increases the biomass of primary consumers in terrestrial ecosystems (McNaughton et al. 1989). However, the way this increase is divided among species and individuals of different sizes is not clear. If plant productivity is to affect animal assemblages in any way it must be due to effects on individual animals. Where energy is available in large quantities for each individual all individuals will have the potential to grow larger and have a higher fitness. Therefore, I expect highly productive sites to harbour more individuals of all sizes, consequently also more species.

## Abundance

Range size has been shown to have a positive effect on abundance Brown, 1984 #460; Gaston, 1988 #461; Maurer, 1990 #347; Gaston, 1996 #86], so species that have large geographic ranges are also on average very abundant within their ranges (Fig. 4). However, the regression coefficients of abundance-range size relationships are commonly in the range of  $r^2 = 0.3$  to  $0.8$ , which implies that a considerable proportion of the variation in abundance cannot be explained by range size. Life-history characters such as the number and size of offspring, longevity and age at independence have been proposed as explanations of the remaining variation (i.e. Blackburn et al. 1997). However, these characters could not satisfactorily explain more than 4% of the remaining variation, which may instead be related to environmental factors such as plant productivity.

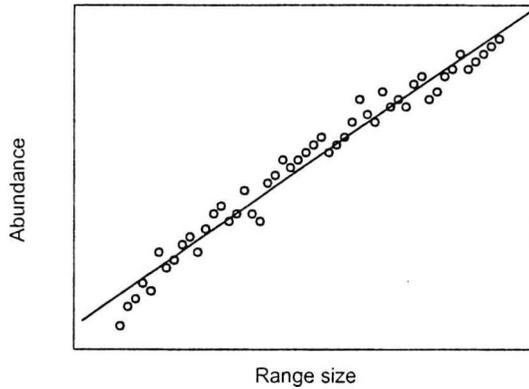


Fig 4. The relationship between species geographical range size and local abundance.

Where plant productivity is low, most species will not have high abundance and the rarest species will probably be completely absent due to high extinction probabilities (Wright 1983). Therefore, the more energy is available, the more individuals and thus the more species there will be. This means that the number of species and the number of individuals in an area should be positively correlated. Also, species that have many high energy habitats within their range may be more abundant than their relatives with similar-sized ranges with a higher proportion of low energy habitats.

## Questions addressed

To achieve the main objective of determining how range size, use of resources, body size and abundance of species are related to productivity at different geographic scales the following specific questions were addressed.

### Range size

*1. Are endemic genera restricted to regions of low plant productivity?*

## **Resource use**

- 2. Will species combine food resources in more ways with increasing plant productivity?*
- 3. Does increasing plant productivity increase the degree of specialisation?*

## **Body size**

- 4. Does the average body mass of species increase with increasing plant productivity?*
- 5. Will there be less variation in body mass where plant productivity is high?*
- 6. Is the relationship between the number of individuals and the number of species within body size classes the same in areas of low and high plant productivity?*
- 7. Does the density of small sized species increase proportionally more than the density of large sized species with increasing productivity?*

## **Abundance**

- 8. Will the abundance of species increase with increasing plant productivity?*
- 9. Are highly abundant species with respect to their geographic range size confined to areas of higher plant productivity than species with low abundance?*

As plant productivity affects different kinds of animal taxa I felt it necessary to include as many higher taxa as possible. However, I also saw the need to do the analyses on taxa that had been well studied in the context of range size, resource use, body size and abundance, and for which different explanations regarding the distribution of these variables had been postulated. Therefore, in the work leading to this thesis I included considerations of mammals (Papers I, II and III), insects (Paper IV) and birds (Paper V). Mammals were chosen for studying range size relationships because we have a fairly good knowledge of the size of mammalian ranges. I also chose Australian mammals because this fauna is well documented

and because the Australian continent is highly varied in plant productivity terms, without being too extended in latitude. Mammalian data on the body size of species were used partly because most previous explanations for the distribution of body sizes were derived using information on mammals. Insect data were used for two reasons. First, they are relatively easy to catch and measure and second, there is a need for data on insects in relation to environmental parameters such as plant productivity. Birds were chosen because they have been well studied in the context of abundance and range size, so derived relationships were relatively easy to compare to results from other studies.

## **Methods**

The main method used in this work was to collect data on species of different taxa from either the literature (papers I, II and III) or from field experiments (papers IV and V) or from and correlate them to relevant plant productivity estimates.

### **Range size**

The influence by net plant productivity on range size was discussed in paper I and all mammalian genera of the world were used for this purpose. There are very good compilations of the mammalian fauna with a global perspective (Wilson & Reeder 1993, Nowak 1999), which enables comparisons to be done at this large scale. However, there are still not sufficiently good data for a large proportion of the species, so these analyses had to be done at the genus rather than the species level.

#### *Study area*

To study if endemic genera are restricted to regions of low plant productivity the 11 major terrestrial zoo-geographical regions of the world were used. These regions differ in geographical extent between  $1.8 \cdot 10^4$  and  $4.7 \cdot 10^7$  km<sup>2</sup> giving a total land area of  $2.8 \cdot 10^8$  km<sup>2</sup>. Due to the large size differences among the terrestrial regions (which vary by more than an order of magnitude) we assigned the regions into two categories; continental regions (six out of eleven) and island regions (five).

### *Species data*

The main sources of species characteristics were Wilson and Reeder (1993) and Nowak (1999). We defined endemic genera as those occurring in one zoogeographic region only.

### *Plant productivity*

The data on net plant productivity (NPP) was taken from a database on net plant productivity (Bazilevich 1994). The estimates are given in ranges for each sub-area of plant productivity within each region so we calculated an unweighted mean of plant productivity for each region.

### *Analyses*

We tested the relationship between mean NPP and the number of endemic genera in island and in continental regions using ordinary least-squares regression.

## **Resource use**

The questions on whether there would be an increase in the number of combinations of food resource use or increasing degree of specialisation with increasing plant productivity were discussed in paper II. I used the herbivorous mammals of Australia because their diets are fairly well known.

### *Study area*

The study area was the mainland of Australia including Tasmania, but excluding other offshore islands, giving a total area of approximately  $7.6 \cdot 10^6$  km<sup>2</sup>. Two thirds of the continent is arid or semi-arid (Strahan 1995). I divided the continent into a grid system with squares  $4 \cdot 10^4$  km<sup>2</sup> sized. A total of 286 squares covered the continent, but 78 squares with smaller land areas at the edges of the continent were excluded from the analysis, giving a total of 208 squares for the analyses.

### *Species data*

Strahan (1995) was the source of information on mammalian species distributions (before the European settlement) in Australia. Of the 285 terrestrial species native to Australia, 152 were included in the study. With a few exceptions, all species included were herbivorous. Each species was classified as using a specific combination of resources. My definition of food resources was based on the type of food each species uses (i.e. the part of the plant which the animal eats). Food resource categories recognised were i) grazed material (monocots and all non-woody dicots), ii) ferns/horsetails/lichens, iii)

roots/bulbs/rhizomes/fungi, iv) browse (leaves/stems/twigs/bark from woody dicots), v) exudates, vi) flowers (pollen/nectar), vii) fruits and viii) seeds. Specialisation can be defined in many ways, but here I define it as adaptation to feed only on a single plant structure such as e.g. roots, nectar or seeds. Therefore, species that used only one resource category were classified as specialists. Information on diets of species was mainly obtained from Strahan (1995), complemented with several other sources (Read 1984, Cronin 1991, Fox et al. 1994, Murray et al. 1999).

### *Plant productivity*

The data on net plant productivity (NPP) was taken from (Bazilevich 1994) and unweighted mean values of productivity for each  $4 \cdot 10^4$  km<sup>2</sup> square was calculated from this source.

### *Analyses*

As the number of species within an area are likely to influence the number of possible food resource combinations the potential effect of species richness on the number of resource combinations was statistically evaluated by a simple linear regression. Residuals from this regression were then regressed against NPP to determine the effect of primary plant productivity on the number of resource combinations. Specialisation was determined in two ways. First, the number of specialist species was plotted against plant productivity. Then, the different types of specialisation were analysed separately to see whether all types would be equally common at all plant productivity levels.

## **Body size**

Questions concerning body size was divided into two sections. First, questions regarding mean and variation of body size were dealt with in paper III and questions about the number of species and number of individuals were answered in paper IV. For clarity I will review the methods used for each paper separately below.

### *Herbivorous mammals*

Paper III is based on the distribution of herbivorous mammals of Australia on the scale of  $10^5$  -  $10^6$  km<sup>2</sup>.

### *Study area*

In Paper III the Australian continent ( $7.6 \cdot 10^6 \text{ km}^2$ ) was divided into seven regions (biomes) of major vegetation type by following Doing (Doing 1970). These biomes ranged in size from  $2 \times 10^5 \text{ km}^2$  to  $2.8 \times 10^6 \text{ km}^2$ . Since the areas were not of the same size I had to correct for this factor in the analyses. Larger areas do include more species and more habitat types (Connor & McCoy 1979). I accounted for this effect by fitting a power relationship of the form

$$\text{Species} = \alpha \text{Area}^\beta$$

between area and number of species, where  $\alpha$  and  $\beta$  are constants.

### *Species data*

Information on the distribution of mammalian species (before European settlement) in Australia was collected from Strahan (1995). A total of 142 terrestrial, herbivorous species native to Australia were considered. Body size was calculated as the mean body mass (in grams) of each species, including both sexes. For approximately half of the species the literature only reported range values, so unweighted averages were used for all species. Body mass was then logarithmically transformed into  $\log_2$  body size classes.

### *Plant productivity*

The data on net plant productivity (NPP) was taken from a model on net plant productivity proposed by Uchijima and Seino (Uchijima & Seino 1985, Seino & Uchijima 1992). This source had previously also been used in studies of termites (Eggleton et al. 1994) and trees (Adams and Woodward 1989). Data regarding plant productivity in the model were given in class ranges, so for each biome I calculated an unweighted average for all range midpoint values included.

### *Analyses*

A frequency distribution of body mass was plotted for each biome. Due to a lack of normality in four out of seven frequency distributions a non-parametric regression test, Kendall's robust line-fit method (Kendall & Gibbons 1990), was used to determine whether there was a monotonically increasing relationship between mean body mass and NPP. This relationship was then tested for significance with Kendall's rank order correlation coefficient (Siegel & Castellan 1988). The same procedure was also used for testing whether there was a monotonically decreasing relationship between variation (standard deviation) of body mass of species and NPP. To ensure that differences between biomes were not simply due to sample size I also conducted a regression test between body

mass and species richness. Placental mammals and marsupials were also considered separately in the same manner as the whole assemblage.

### *Insects*

Questions regarding number of species with number of individuals and whether there will be an increase in numbers of individuals and species in different size classes with increasing plant productivity were discussed in paper IV, which considers the local scale.

### *Study area*

I used young forest sites of approximately 3-5 ha each in the coastal and inland areas (about 64° N and 20° E) in the county of Västerbotten in northern Sweden. The forests had been clear-cut 10 years prior to the study.

### *Species data*

I collected insects by using pit-fall traps in a  $1.5 \cdot 10^{-2}$  km<sup>2</sup> grid system over the clear-cut. Two hundred and fifty traps per site were placed 10 m apart. Collections were conducted during July and August 1999. The species were later identified to species, counted and measured (length). The total length of each individual (in mm) was considered as the distance from the mouth-parts to the end of the abdomen for rove beetles and to the end of the elytra for ground beetles. Length was measured using an optical micrometer. Total length was then logarithmically transformed into  $\log_2$  body size classes by the same method as Siemann (1996) except for class division. Body size classes were divided so that a class of size N included individuals or species ranging in length from  $2^{N-0.5}$  mm up to, but not including  $2^N$  mm. This gave seven body size classes ranging from  $2^{1-1.5}$  to  $2^{4+4.5}$ .

### *Plant productivity*

Plant productivity data for the sites were not available, but I used the stem volume production of trees estimated as m<sup>3</sup> per hectare per year (2001). The estimate was retrieved from the company that owns the forest (ASSI Domän).

### *Analyses*

The number of species in each size class was plotted against the number of individuals of the same size class for each forest site, and a linear or polynomial regression was fitted to the relationship to find the best fit. This was done to find out if there would be any consistent change in the form of this relationship with increasing plant productivity.

Plant productivity of the sites were then related to the density and species richness of each size class by an ordinary linear regression to test whether there would be an increase in density and species richness in all size classes with increasing plant productivity.

## **Abundance**

Finally, questions of increasing abundance with plant productivity and if species with higher abundance than expected by their range size would be distributed within the most productive areas were addressed in Paper V. Here the focus was on the breeding bird fauna of Sweden because of two reasons. Birds has been extensively studied and Sweden has an extensive database on forest production throughout the country that gives an excellent opportunity to relate data on bird distribution to.

### *Study area*

The study area considered here was Sweden ( $4.5 \cdot 10^2 \text{ km}^2$ ). Sweden include alpine regions with a tundra climate, through boreal forests to deciduous forests in the temperate zonet. Sweden was divided into a grid system with  $625 \text{ km}^2$  squares based on the National Swedish Grid with a total of 960 squares covering the country. Of these, 336 squares were included in the breeding bird survey.

### *Species data*

Bird data, collected by the Swedish Ornithological Society in a survey of the number of breeding birds in Sweden was used here. The survey is conducted each year during the breeding period, from May to the first week of July depending on geographic location. The data in this study comes from surveys done in the years 1996 to 2000. The survey recorded 224 species in total for all years. There was a slight bias in the geographical representation of the monitoring, with a higher number of squares monitored in the south than in the north.

Of the 224 species only forest related species (122) were used as the source of population estimates and also for range size estimates. The birds were monitored using a combination of transects and points. Each sample count, located near the centre of a  $625 \text{ km}^2$  square of the national grid, consisted of all birds recorded (heard or seen) along an eight km long line transect and at eight points evenly distributed along the transect. The data obtained from the combined transect/point count gave the total abundance for each year in each  $625 \text{ km}^2$  square. A mean abundance for each year was then calculated. Range size was measured as the number of  $625 \text{ km}^2$  squares. Both abundance and range size were  $\log_{10}$  transformed in these analyses.

### *Plant productivity*

As a rough index on plant productivity we used stem volume of trees (in m<sup>3</sup>) produced within a hectare each year. The source of this information was the Swedish National Forest Inventory (<http://www-nfi.slu.se2001>) collected and distributed by the Department of Forest Resource Management and Geomatics at the Swedish University of Agricultural Sciences in Umeå. Staff here systematically monitor forest productivity every year throughout Sweden. Each 625 km<sup>2</sup> square included several observations on stem volume production, but for the purpose of paper V only a mean value for each square was used.

### *Analyses*

Mean log abundance of each species were first regressed against log range size and the residuals were then classified categorically according to their sign (positive or negative). These categories were analysed with respect to mean stem volume of trees in a pair-wise comparison using one-tailed t-test.

## **Results and Discussion**

### **Range size**

#### *Are endemic genera restricted to regions of low plant productivity?*

The majority (64 %) of the now living 1153 mammalian genera was considered as endemic (Paper I). We found that numbers of genera endemic to continental regions showed a weak, positive relationship with plant productivity ( $Y = 40.29 + 5.85X$ ;  $r^2 = 0.14$ ,  $p = 0.46$ ,  $N = 6$ ; paper I: fig. 1), while endemic genera occupying island regions showed a weak negative relationship with productivity ( $Y = 108.44 - 3.79X$ ;  $r^2 = 0.62$ ,  $p = 0.11$ ,  $N = 5$ ; paper I: fig. 2). The relationships were thus inconsistent. Furthermore, while the relationship for island regions supported our predictions that endemic genera should be depressed by high levels of plant productivity, the relationship for continental regions disagreed with the predictions. However, as island regions are on average more productive than continental regions, these results suggest that there could be a hump-shaped relationship (see Fig. 1c in the Introduction) between numbers of endemic species and productivity, with endemic genera being most common in intermediately productive regions. A hypothesis that may explain this pattern is the 'environmental heterogeneity' hypothesis, as discussed in the Thesis *Introduction*. Highly productive islands may be too homogenous in terms of plant species. Plant diversity at the regional to global scale (200 to >4000 km) have been shown by some to peak at intermediate plant productivity (Waide et al.

1999). Suppose that species belonging to endemic animal genera are not capable of exploiting resources with sufficient efficiency to maintain viable populations under these circumstances. As plant productivity decreases, these species might have the capacity to become more abundant due to increasing heterogeneity of resources. At still lower plant productivity levels the environment becomes homogenous again, due to the lower abundance and diversity of plants. Because of this, total species and generic richness will be low and consequently the number of endemic genera will be low as well. This implies that endemic genera are only indirectly affected by plant productivity, via habitat heterogeneity.

*Thus, endemic mammalian genera cannot be considered to be restricted to regions of low plant productivity, instead they are probably most common in regions of intermediate productivity.*

## **Resource use**

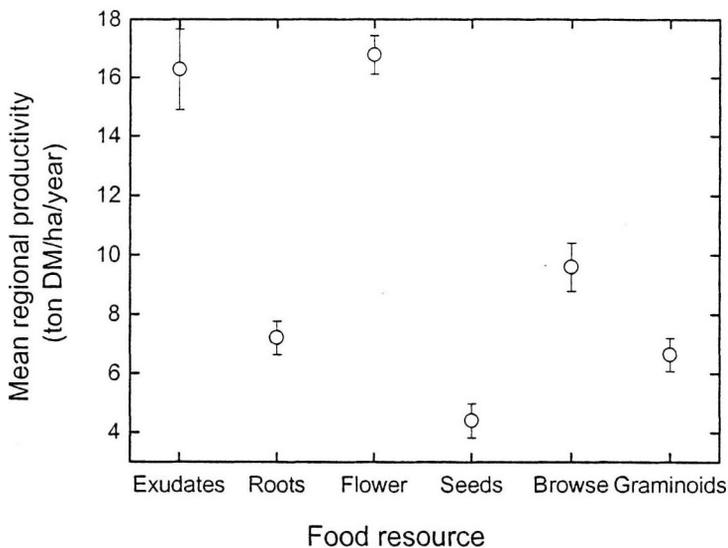
*Will species combine food resources in more ways with increasing plant productivity?*

The number of food resource combinations was closely related to the species richness ( $r^2 = 0.83$ ,  $p < 0.001$ ,  $n = 208$ ) of Australian herbivorous mammals (Paper II). Of the remaining variation in the number of resource combinations, plant productivity could only explain an additional 2% ( $r^2 = 0.02$ ,  $p < 0.001$ ,  $n = 208$ ). Thus, plant productivity does not seem to affect resource use at this scale, at least not in the way resource use was estimated. Rosenzweig (1995) claimed that as the number of species within an area increases, the number of possible habitats also increases because species will discriminate between habitats in more ways. This may also be the case for food resources here and it is probably why the results are not straightforward.

*Thus I could not find any evidence that Australian herbivorous mammals do not use resources in more combinations in regions of high plant productivity than in regions of low productivity.*

*Does increasing plant productivity increase the degree of specialisation?*

The degree of specialisation among Australian mammals (Paper II) is affected by energy availability, but it is approximately equal in low and high productivity regions, and lower in intermediately productive regions. The main differences between the low and high productivity regions lie in the type of food resource that is selected. In low productivity regions species are mainly specialists on seeds, roots and grass, while in highly productive regions exudates and flowers are the selected food resource categories (Chi-square = 109.78,  $df = 5$ ,  $p < 0.0001$ ; Fig. 5).



*Fig. 5* Resource categories that Australian mammal species specialise upon and the mean plant productivity ( $\pm$  se) of the regions where these resource categories are most commonly used by specialists.

According to the hypothesis of increasing specialisation (see hypothesis 3 in the *Introduction*) there should not be any specialist species where plant productivity is low because the resources they rely upon should not be sufficiently abundant to support viable populations. However, we see here that for root, grass and seed specialists this does not hold true, probably because these resource are not most abundant where plant productivity is high. Instead they become increasingly uncommon as plant productivity increases, due to changes in landscape structure. Therefore, I cannot in this case support the hypothesis that specialisation increases with increasing plant productivity.

*To summarise, species of Australian herbivorous mammals are not more specialised in regions of high plant productivity than in regions of low productivity. The type of specialist species differs instead, with more root, grass and seed specialists in low productive regions, and more exudate and flower specialists in high productive regions.*

## Body size

*Does the average body mass of species increase with increasing plant productivity?*

Mammals in highly productive biomes of Australia had a larger mean body mass than mammals in low productivity biomes (non-parametric regression,  $Y = 8.337 + 0.074X$ ; Kendall  $T = 0.714$ ,  $P_{(\text{one-tailed})} = 0.015$ ,  $N = 7$ ; paper III: fig. 2c). Except in the South-eastern savanna biome, there is a general trend for species to become heavier where available energy levels are higher. The south-eastern savanna biome consists of open woodland and grasslands (Bridgewater 1987), which suit grazers best. Since the majority of grazers in Australia are large-sized macropods, the high mean body mass in this biome probably reflects the fact that this habitat is best suited to these species.

The Australian herbivorous mammal fauna consists of two major taxa with separate origins, the placentals and the marsupials. The placental mammals are dominated by small-sized orders, mainly Rodentia (rodents), and Chiroptera (bats), while marsupials tend to be found among the larger size classes but have greater variation in their size distribution. Therefore, it was also important to analyse each major taxon separately. However, while mean rodent body size significantly increased with increasing plant productivity (non-parametric regression,  $Y = 5.745 + 0.051X$ ,  $T = 0.810$ ,  $P_{(\text{one-tailed})} = 0.005$ ,  $N = 7$ ) there was no corresponding increase among marsupial masses ( $Y = 11.273 - 0.003X$ ,  $T = -0.048$ ,  $P_{(\text{one-tailed})} = 0.500$ ,  $N = 7$ ). This indicates that it is among small sized species that plant productivity can lead to an increase in size.

*In conclusion, the average body mass of Australian herbivorous mammals does increase with increasing plant productivity. However, this increase is only significant for rodents, which are small sized and not for marsupials, which mainly occupies larger size classes.*

*Will there be less variation in body mass where plant productivity is high?*

The total variation in the body size of mammals in Australian biomes decreased with plant productivity (nonparametric regression  $Y=3.459-0.019X$ , Kendall  $T=-0.619$ ,  $P_{(\text{one-tailed})}=0.035$ ,  $N=7$ ; paper III: fig. 2a). More plant productivity could thus mean more energy is available for growth. The variation in sizes was not affected as the rodents and marsupials were analysed separately (Rodents;  $Y=1.544-0.012X$ ,  $T=0.238$ ,  $P_{(\text{one-tail})}=0.281$ ,  $N=7$ . Marsupials;  $Y=2.204+0.008X$ ,  $T=0.238$ ,  $P_{(\text{one-tailed})}=0.281$ ,  $N=7$ ). In a large sample of species there is a greater chance of finding extreme body size values than in a small sample. As the most species rich biomes were also the most productive, they could have shown a

larger variation of sizes simply because of random sampling. The reason the variation of sizes is not affected when each taxon is considered separately is probably because the sample size is too small to detect any difference.

*To summarise, the variation of body masses of Australian herbivorous mammals does decrease as plant productivity rises. However, for rodents the decrease was not statistically significant, and for marsupials the variation increased slightly.*

*Is the relationship between the number of individuals and the number of species within body size classes the same in areas of low and high plant productivity?*

The form of the relationship between the number of species and the number of individuals (paper IV: table 2) among body size classes was studied for two families of ground dwelling coleopterans, ground beetles (Carabidae) and rove beetles (Staphylinidae). In the most productive site (Ralberget) and in one of the second most productive (Djupsjöbränna) the relationship was best described by a linear function. In sites of lower plant productivity, and in Mörtsjöstavaren (the other site of high productivity) the relationship was best described by power functions ( $S = \alpha I^\beta$ ) with powers between 0.6 and 0.83. This suggests that the relationship of  $S = I^{0.5}$  proposed by Siemann et al. (1996) also applies to ground beetles and rove beetles of young forests in northern Sweden. The sites for which the relationship was linear contained fewer individuals within the size class with the highest number of individuals than it did in Mörtsjöstavaren, where the relationship was described by a power function. Therefore, it is more likely that the true relationship for all sites, irrespective of how productive they are, can be described by a power function. The consequences this has is that in size classes that are far from the asymptote an increase in number of individuals will also increase the total species richness in an area. If the increase of individuals is in a size class that is at the asymptote, overall species richness will not increase. This is not affected by productivity. What productivity may affect is the rate at which this saturation point is reached and the number of species that is included within this saturation point.

*Thus, the number of different sized species of ground dwelling coleopterans increase with the same rate with increasing number of individuals irrespective of plant productivity of the habitat.*

*Does the density of small sized species increase proportionally more than the density of large sized species with increasing plant productivity?*

The number of large sized individuals (size class  $2^{4-4.5}$ ) of ground dwelling Coleoptera in local forest sites increased with increasing plant productivity, while

the number of individuals of smaller size decreased instead (Table 5 in paper IV). For species it was instead within the smallest size class  $2^{1.5-2}$  that the number of species increased, while the rest, including the largest, decreased. However, none of these relationships were significant. As the results are not statistically significant, I cannot conclude that there are real differences between size groups. But, if these trends can be confirmed by further studies, then they suggest that with increasing plant productivity there will be more intense competition between species of large size, with increased dominance by the most common species. Further, there may be intense competition among species in the smallest size class, thereby keeping all species in low abundance but allowing for more species to co-exist. This does not support the findings of Cyr et al. (1997), i.e. that small sized species in aquatic communities increased at a faster rate with plant productivity than did large sized species. However, further studies need to be made before we can draw any general conclusions about the relationship between numbers of individuals and numbers of species of different size.

*To summarize, the number of individuals of small size tended to decrease, but the number of species tended instead to increase with increasing plant productivity. In contrast, the number of large sized individuals increased while the number of species decreased when productivity increased.*

## **Abundance**

*Will the abundance of species increase with increasing plant productivity?*

The average abundance of bird species in local forest sites in northern Sweden was lowest at intermediate levels of tree stem volume ( $Y = 0.60 - 0.005X + 0.00004X^2$ ;  $r^2 = 0.04$ ;  $p = 0.002$ ;  $n = 316$ ; fig. 1 in paper V) and increased at sites with both lower and at higher plant productivity. Thus, plant productivity has an effect on abundance of Swedish breeding birds, although they are not positively related as suggested by the 'energy limitation' hypothesis (hypothesis number one in *Introduction*). These relationships can partly be explained by the following observations. Firstly, species with high abundance in low productivity sites tend to have a more northern distribution while species with high abundance in high productivity sites have a more southern distribution. Secondly, species that are the most abundant in intermediate productivity sites have larger ranges than the groups found in either extremes of productivity, thus they are observed in areas spanning a wider variation of plant productivity. However, there is also the possibility that local abundance is not energetically controlled. Warren and Spencer (1996) for example noted that although taxonomic richness of algal communities was higher at high energy levels the number of individuals was lower. Further, Srivastava and Lawton (1998) could not find any consistent

relationship at all between productivity and numbers of species for tree-hole communities of invertebrates.

*Consequently, the abundance of breeding bird species in Sweden do not increase monotonically with increasing plant productivity. Instead the abundance first tends to decrease and then increase with increasing plant productivity.*

*Are highly abundant species with respect to their geographic range size confined to areas of higher plant productivity than species with low abundance?*

Range size of breeding birds in Sweden explained half of the variation in mean local abundance ( $Y = -0.51 + 0.41X$ ;  $r^2 = 0.50$ ;  $F = 116.46$ ;  $p < 0.0001$ ;  $n = 119$ ; paper V: fig. 3). The variation was then divided into two categories; negative (species with lower abundance than expected according to their range size), and positive (species with higher abundance than expected). We predicted that the positive category would be found in higher productivity forests on average than the negative category. However, contrary to our predictions species in the former category were on average represented in areas with higher stem volume productivity than the latter (positive,  $56.46 \pm 2.59$  and negative,  $65.27$ , one-tailed t-test,  $t_{117} = -2.19$ ,  $p = 0.03$ ). However, if we assume that abundance is not energetically controlled, then it is not surprising that species with a higher than expected average abundance tend to be found at lower plant productivity than species with lower than expected abundance. Even if abundance is energetically controlled, it seems to favour species that are uncommon.

*To summarise, species with higher abundance than expected according to their range size tend to be found in forests of lower productivity on average than species with lower than expected abundance, not in forests of higher productivity.*

## Conclusions

A summary over the variables that were studied and their relationship with productivity is presented in Table 1. The relationships found between plant productivity and the variables presented in this thesis are not always as expected. Instead there is considerable variation among them in this respect, some show a clear relation to productivity while others do not. I had hoped to find simple connections between these variables, but this does not seem to be the case. However, neither the mean abundance of species (paper V) nor the frequency of sizes (paper IV) were positively affected by plant productivity. Since these studies were on a relatively small scale (local) these results indicate that density of species may not be dependent on energy availability, or at least the pathways

of energy transfer from plants to these species that to a large extent are secondary consumers is not straightforward. Therefore, I find it difficult to accept the 'energy limitation' hypothesis (hypothesis number one in Introduction). The results of the range size analysis give no grounds for dismissing the 'habitat heterogeneity' hypothesis (hypothesis number two in Introduction). However, if this hypothesis is valid the number of combinations of resources should have been largest at intermediate productivity levels, which was not the case. The 'more specialisation' hypothesis was not supported for mammals of Australia either.

Table 2. Summary of how the variables presented in the thesis are related to plant productivity ( $Y=PP$ ). The geographical scale at which the variables were studied is also shown.

Taxon	Scale (km <sup>2</sup> )	Variable (Y)	Y = PP
Mammals	1.8·10 <sup>4</sup> - 4.7·10 <sup>7</sup>	Range size (endemics)	= <sup>1</sup>
Mammals	4·10 <sup>4</sup>	Resource use (combinations)	0
Mammals	4·10 <sup>4</sup>	Resource use (specialisation)	= <sup>2</sup>
Mammals	2·10 <sup>5</sup> - 2.8·10 <sup>6</sup>	Body size (mean)	+
Mammals	2·10 <sup>5</sup> - 2.8·10 <sup>6</sup>	Body size (variation)	-
Insects	1.5·10 <sup>-2</sup>	Body size (S = I)	0
Insects	1.5·10 <sup>-2</sup>	Body size (density and richness)	+/-
Birds	6.25	Abundance (mean)	= <sup>2</sup>
Birds	6.25	Abundance (positive residual)	-
Birds	6.25	Abundance (negative residual)	+

(=<sup>1</sup>) The relationship is unimodal with highest numbers at intermediate plant productivity.

(=<sup>2</sup>) The relationship is antimodal with lowest numbers at intermediate plant productivity.

(+) Positive relationship.

(-) Negative relationship.

(0) No effect.

To summarise, the spatial scale at which the relationships between productivity and species characteristics were observed certainly influenced the results. However, there were also taxonomic and functional differences between these organisms, which clearly also affected the relationships observed.

In conclusion, the effect of plant productivity on species characteristics such as range size, resource use, body size and abundance is complex and sometimes the pathways are not evident. I do still believe that if species richness is functionally dependent on plant productivity then plant productivity must also have an effect on these attributes. However, changes in productivity are likely to induce complex interactive changes in all key attributes, rather than clear linear responses.

## Future perspectives

As an example of how possible future studies may help us understand the interactions of these variables' relationships to plant productivity, I will consider the relationships between the number of endemic genera and the number of specialist species. The number of endemic mammalian genera was highest at intermediate plant productivity levels, while food specialist mammalian species were more common when productivity was either low or high. At this stage these relationships are not directly comparable due to differences in scale and taxonomic level. However, if only endemic species were tested for the degree of specialisation and for commonness on the scale that specialisation among species were considered here, we could begin to evaluate how the two variables affect each other's relationship with plant productivity. If the trends have a similar pattern to those shown for all herbivorous mammals, then we can say that specialisation among endemic species requires the environment to be either unproductive or highly productive. These ideas are merely speculations and they have to be carefully tested before we can draw relevant conclusions with any certainty.

As plant productivity has been shown to have an effect on species richness at all possible scales there are bound to be mechanisms operating at all scales (Scheiner et al. 2000) but they are not likely to be the same. Therefore, it would be valuable to investigate the effect of plant productivity on all the proposed response variables mentioned above at all possible geographic scales.

It is, further, important not to forget that all the variables discussed in this thesis are often highly correlated and dependent upon each other (Blackburn & Gaston 2001). This can be done by for instance studying complete communities and to examine all these response variables at the same time but at only one scale in created miniature ecosystems, microcosms. By this we can combine the present approach with for instance ecosystem ecology, which concerns various interactions between organisms and their environment.

We can also use an experimental approach where factors associated with plant productivity can be varied in a controlled manner (Rosenzweig and Abramsky 1993). However, as this can only be done at relatively small spatial scales interpretation of the results is still prone to uncertainty and extrapolation is still required when considering larger spatial scales (Brown 1995).

Unfortunately for a majority of the taxa alive today we have, very limited autecological knowledge (Gaston & Blackburn 1999) so for these taxa further data are essential if we want to make proper comparisons between taxonomic units. Food resource use is also very difficult to analyse in this context and careful decisions about how to estimate resource use and resource preferences at different spatial scales are vital for clear analyses. Therefore, even though I

strongly believe that in order to fully understand how plant productivity affects species we need to know how species relate to their food supply and how food resources are related to productivity, I do not think that at this stage we really have the data necessary for this purpose.

Further, incorporating phylogenetic independent comparisons in the analysis may also be worth the effort, since closely related species are more similar in nearly all characteristics than more distant ones, as the traits of related species are constrained by those of their ancestors (Harvey & Pagel 1991). Using phylogenetic comparisons can remove this effect. I have consequently chosen not to include this method in my analyses because for some taxa the phylogeny has still not yet been fully resolved.

I have in this thesis focused on the mechanisms behind the relationship between productivity and species richness. As could be seen the links were often not obvious. This implies that these attributes have a complex connection to plant productivity. It also implies that plant productivity is likely to be tightly connected to other factors, e.g. habitat heterogeneity, area and latitude, which also have an influence on species characteristics. Therefore, I believe that we need to consider all possible attributes of species in conjunction.

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